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Relationships among the Four Species of the Superspecies *Celeus elegans* (Aves, Picidae)

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ABSTRACT

Four allospecies (semispecies *auct.*), *castaneus*, *elegans*, *lugubris*, and *flavescens* comprise the superspecies *Celeus* [*elegans*] *elegans*. These species share basic color patterns, bill structure, and proportions setting them apart from related species of *Celeus*. *Celeus lugubris* frequently has been merged in *C. flavescens*, but these two species approach each other closely in their distribution without apparent interbreeding. In contrast, at least two hybrids of *C. lugubris* x *C. elegans*, which barely meet in Mato Grosso, indicate their close relationship. *Celeus flavescens ochraceus* meets and overlaps somewhat with *C. elegans jumana* in northeastern Brazil without interbreeding. *Celeus castaneus* a monotypic Middle American species is related most closely to *C. elegans*, although showing some peculiar features. *Celeus flavescens* probably is an older, and *C. lugubris* a somewhat younger, independent derivative of an ancestor in common with *C. elegans*. Variation in *C. elegans*, *C. flavescens*, and *C. lugubris* suggests that introgressive hybridization may have affected all three species in the past, and may be affecting *C. lugubris lugubris* today. *Celeus elegans* and *C. flavescens* are strongly polytypic, with distinct races or racial groups in secondary contact. *Celeus lugubris* is polytypic, with two moderately marked races.

INTRODUCTION

Neotropical species of the genus *Celeus* are among the least known of New World woodpeckers. Most species are chestnut or rufous in color,

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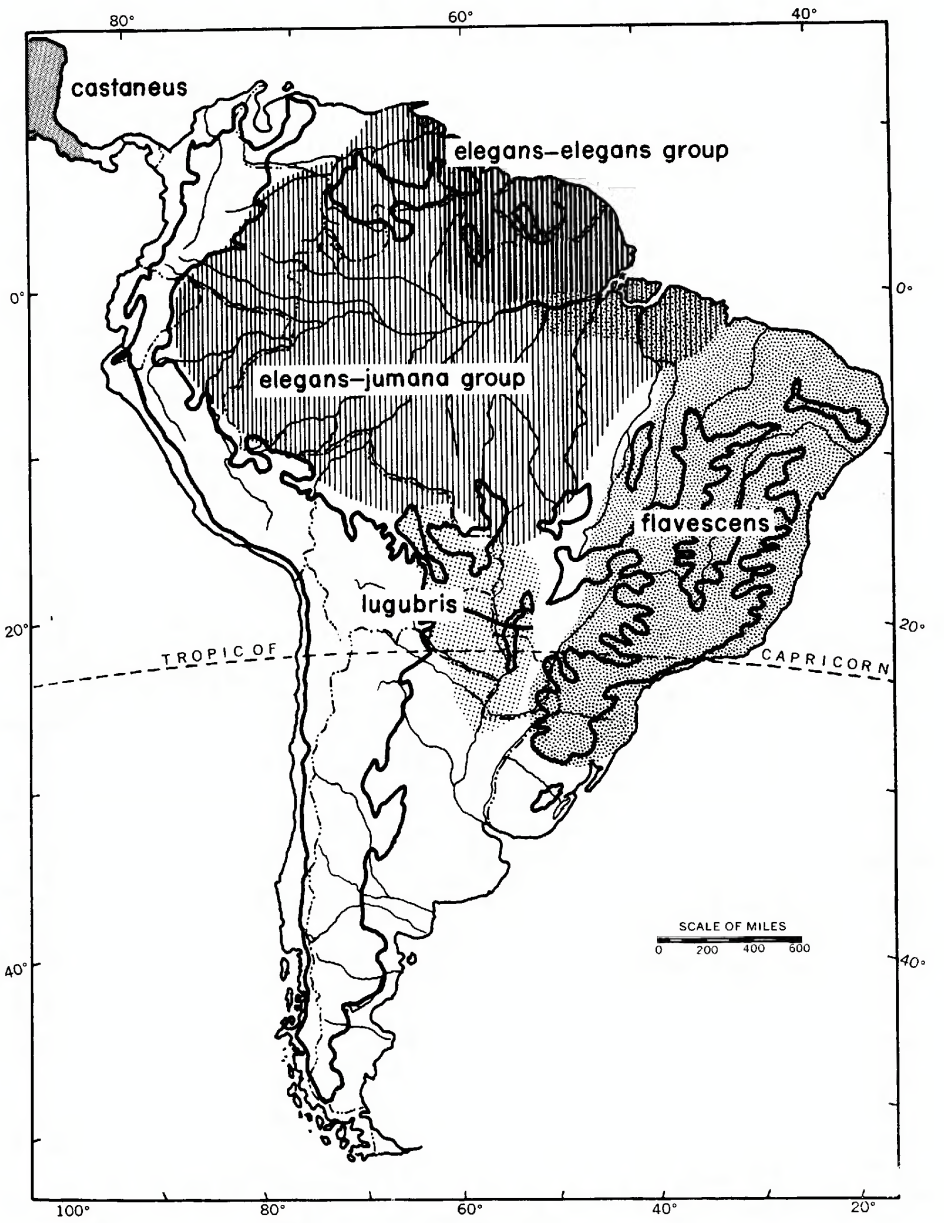

FIG. 1. Ranges of species of the *Celeus elegans* superspecies. *Celeus castaneus* extends through Middle America to Mexico. The horizontal black line through the range of *C. lugubris* is the approximate boundary between northern *C. l. lugubris* and southern *C. l. kerri*. Note especially the contact between *lugubris* and *elegans* (*jumana* group) in Mato Grosso, and overlap of *elegans* (*jumana* group) with *flavescens* in northeastern Brazil.

and all are rather quiet, inconspicuous birds of mainly dense forests. Most if not all of these woodpeckers are ant-foraging species, spending relatively little time tapping to break into an ant nest or subsurface tunnel, and spending much time probing and "tonguing" up ants in the openings they have made. The present report is an attempt to clarify the relationships among one group within the genus, namely the superspecies comprised of the allospecies (Amadon, 1966; semispecies, *auct.*) *castaneus*, *elegans* (including *jumana*), *lugubris*, and *flavescens*. I preface the results of my studies with a list of the species of *Celeus*, arranged according to unpublished investigations by W. Bock and myself. The species of *Celeus* are as follows:

Celeus (*Micropternus*) *brachyurus*
Celeus loricatus
Celeus [*undatus*] *undatus*
Celeus [*undatus*] *grammicus*
Celeus [*elegans*] *castaneus*
Celeus [*elegans*] *elegans*
Celeus [*elegans*] *lugubris*
Celeus [*elegans*] *flavescens*
Celeus flavus
Celeus spectabilis
Celeus torquatus

Brackets indicate superspecies, following Amadon (1966). The authors and citations for these species can be found in Peters (1948). All species of *Celeus* are strictly tropical in distribution; *brachyurus* inhabits Southeast Asia, and the remainder of the species occur in the Neotropics, a pattern of distribution paralleling that found in the piculet genus *Picumnus*.

Species of the *elegans* superspecies are distributed (fig. 1) in Central America (*castaneus*), the Amazonian and northeastern South American lowlands (*elegans*, including *jumana*), the chaco and southwestern cerrado (*lugubris*), and eastern and southeastern Brazil (*flavescens*, including *ochraceus*). The close relationship of *lugubris* and *flavescens* is generally acknowledged, as these frequently are treated as conspecific (Peters, 1948; see also Meyer de Schauensee, 1966). Although *elegans* and *castaneus* usually are placed near *flavescens* and *lugubris* in classifications (e.g., Peters, 1948), they have not been treated previously as geographical representatives. All four species of the superspecies are illustrated in figures 2 and 3.

METHODS AND MATERIALS

About 800 specimens formed the basis for this investigation. Standard measurements obtained were: wing length (chord); tail length; bill length (from nostril); and tarsal length. Other measurements taken are as noted below.

Specimens were studied in the following collections, or were obtained on loan from these institutions:

AMNH, the American Museum of Natural History
ANSP, Academy of Natural Sciences of Philadelphia
BM, British Museum (Natural History)
CM, Carnegie Museum
FMNH, Field Museum of Natural History
MACN, Museo Argentino de Ciencias Naturales
MAK, Museum Alexander Koenig
MCZ, Museum of Comparative Zoology, Harvard University
NHMW, Naturhistorisches Museum, Vienna
NMM, Naturhistorisches Museum, Munich
SM, Senckenberg Museum, Frankfurt
SMNH, Swedish Museum of Natural History
UMMZ, University of Michigan Museum of Zoology, Ann Arbor
USNM, National Museum of Natural History, Smithsonian Institution

My field experience with the species of the *Celeus elegans* group is limited to *C. lugubris kerri*, which was studied in Corrientes and Formosa, Argentina, during 1967 and 1968.

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and Mr. Derek Goodwin at the British Museum (Natural History), London.

THE SUPERSPECIES *CELEUS ELEGANS*

The *elegans* superspecies is characterized by the bill, and by what for *Celeus* is rather great variation in plumage coloration. *Celeus elegans*, *C. flavescens*, *C. lugubris*, and *C. castaneus* have proportionally and structurally similar bills, with a moderately curved culmen, a small chisel-tip, and weak nasal ridges. *Celeus grammicus* and *C. undatus* have bills much like those of the *elegans* group, but proportionally much shorter (e.g., *C. grammicus* is similar in size to *C. castaneus*, but the bill is very much smaller and shorter). *Celeus flavus* has a bill like that of the *elegans* superspecies but it is more curved at the culmen, which is exceedingly ridged, and the nasal ridges are obsolete (these differences, and those between *grammicus-undatus* and the *elegans* superspecies, may help to allow the broad sympatry of *flavus*, *grammicus*, and *undatus* with species of the *elegans* group). Asian *C. brachyurus* resembles the *elegans* superspecies in the bill, but the bill tends to be narrower between the nares and, like *flavus*, the nasal ridges are very weak. The bills of the other species of *Celeus* (*loricatus*, *torquatus*, and *spectabilis*) are somewhat to much straighter, with more pronounced chisel-tips, and stronger nasal ridges than those of the superspecies *elegans*. The specialized bills of *loricatus*, *torquatus*, and *spectabilis* may account partly for their broad sympatry with various other species of *Celeus*.

Judging from the shape of the bill and variation in plumage patterns, the *elegans* group appears to occupy a central position within the genus. Color patterns, bill structure, and foot structure suggest the close relationship of the *elegans* superspecies with *C. flavus* on the one hand, and with *grammicus-undatus* on the other. *Celeus flavus* frequently shows a tendency to rufous coloration on its body feathers; a pronounced tendency of this sort would render it like *C. elegans* in appearance. Indeed, its yellow-white coloration may have evolved under the influence of interactions with *C. elegans*, with which it is broadly sympatric. *Celeus grammicus* and *C. undatus* are more barred, smaller, and have a smaller bill than that of the superspecies *elegans*. But their overall coloration, including unmarked, pale sides and tendency to a rump patch in *grammicus* and a similar-shaped bill to that of the *elegans* group suggest close relationship with that superspecies. Relationships of the superspecies *elegans* with the other species of *Celeus* are more distant; I note, however, that the bill structure and coloration of *C. spectabilis* suggest its somewhat intermediate position, and perhaps relationship between *torquatus* and the *elegans* group. Further discussion of relationships within *Celeus* is beyond the scope of the present report.

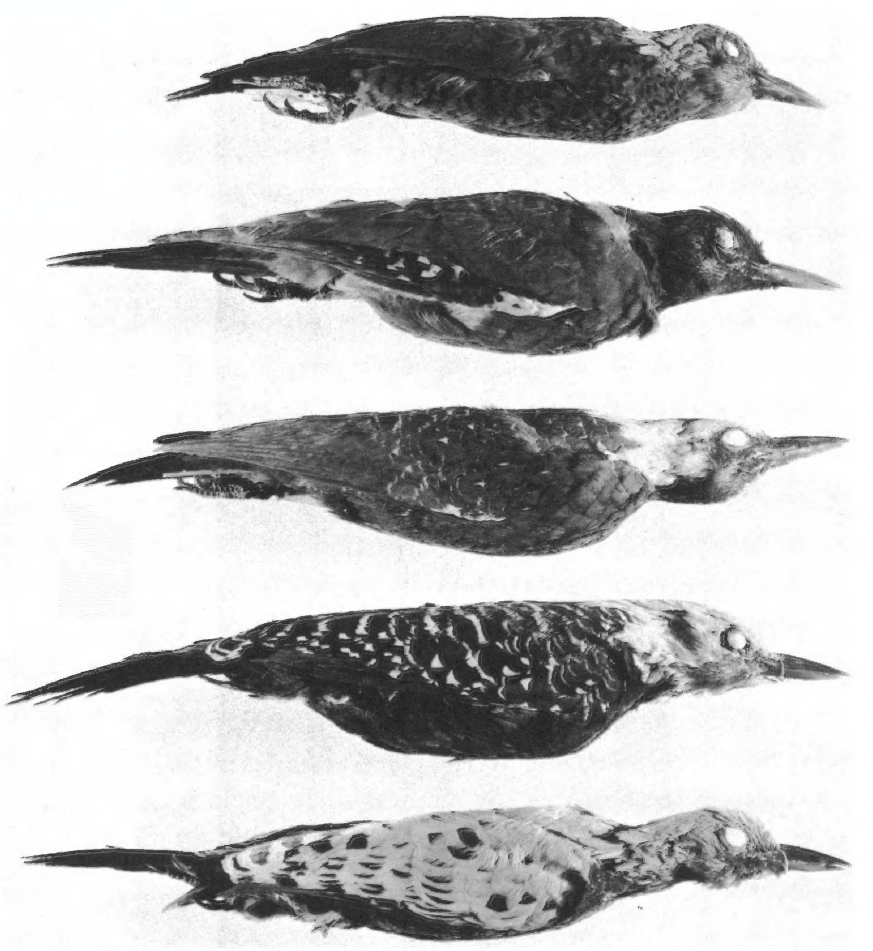

FIG. 2. Male specimens of species of the *Celeus elegans* superspecies, side view. From the top downward are: *Celeus castaneus* from Nicaragua (tail inordinately shortened in preparation of the specimen); *Celeus elegans jumana* from Rio Tocantins, Brazil; *Celeus lugubris kerri* from eastern Paraguay; *Celeus flavescens flavescens* from eastern Paraguay; and *Celeus flavescens ochraceus* from Maranhão, Brazil. The bottom specimen is 280 mm. in length. Note especially the shape of the bill and the extent of barring on the back (and underparts of *C. castaneus*). (See text and figure 3.)

At this point a brief comparison of the species of the *Celeus elegans* superspecies is in order (see table 1); summaries of their geographic variation also are included.

Celeus [*elegans*] *castaneus* (Wagler)

This is the smallest allospecies of the *elegans* superspecies (wing length

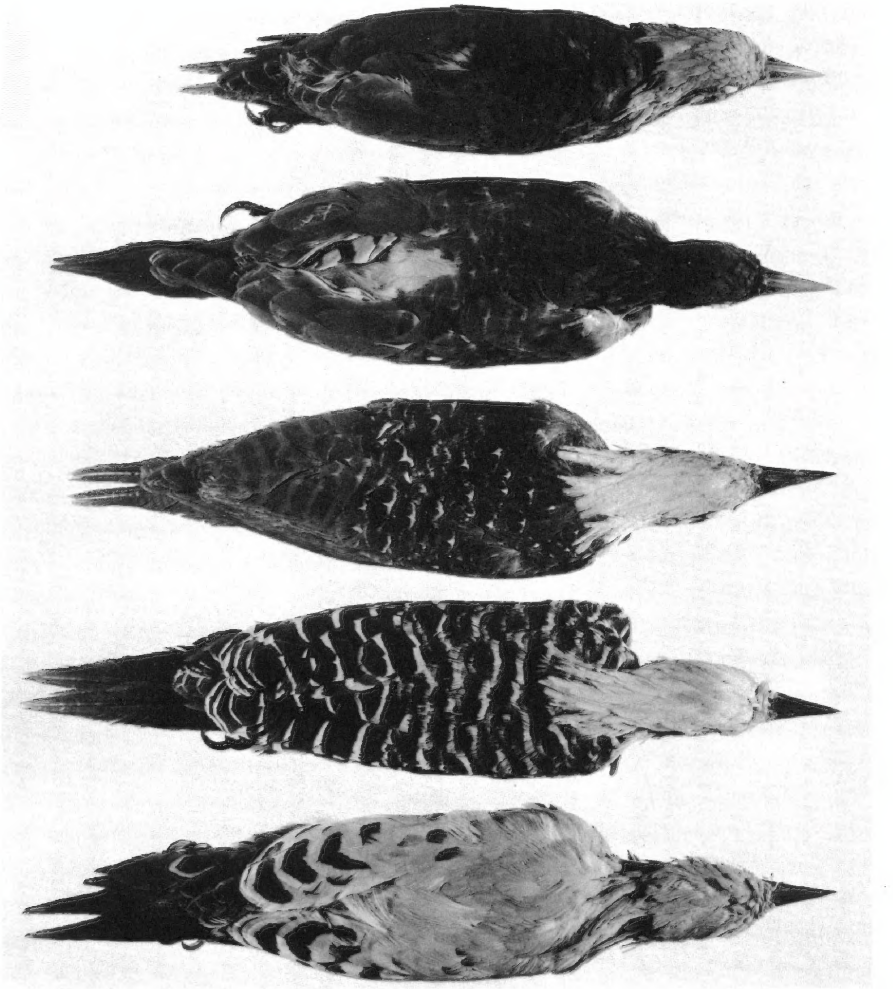

FIG. 3. Male specimens of species of the *Celeus elegans* superspecies, dorsal view (same birds as fig. 2). From the top downward are: *Celeus castaneus* (tail inordinately shortened in preparation of the specimen), *Celeus elegans jumana*, *Celeus lugubris kerri*, *Celeus flavescens flavescens*, and *Celeus flavescens ochraceus*. The bottom specimen is 280 mm. in length. Note especially shape and color of the bill, extent of back barring, and color of the crest, which is (from top to bottom) pale cinnamon, chestnut, white, creamy white, and buff. (See text.)

about 130 mm.); it occurs in Central America from Mexico to Panama (fig. 1). It does not come into contact with *C. elegans*, the most proximal species of the group, and the species which it resembles most closely (table 1). *Celeus castaneus* is monotypic, but shows much individual variation.

Except for dorsal and ventral barring, and the red loral, subocular,

and (sometimes) crown and throat markings of males, this species may be regarded as a diminutive version of *C. elegans*. *Celeus lugubris* and *C. flavescens* show strong tendencies for ventral (flanks) barring, and both, as well as *C. elegans*, show dorsal barring to some extent. *Celeus flavescens*

TABLE 1

A Color Comparison of Species of the *Celeus elegans* Superspecies[a]

Character	*Celeus castaneus*	*Celeus elegans*	*Celeus lugubris*	*Celeus flavescens*
Crest	moderately long	long or short	long	long
Head color	chestnut to buffy	chestnut; crown may be pale buff	blonde; dark face marks	cream or blonde; face marks small
Back color	chestnut and black barred	chestnut; some barring in some	sooty to rufous; barred, light bars narrow	black and white barred, or rusty white, black checks
Ventral color	chestnut; barred	chestnut; unbarred	sooty black to rusty; bar traces	black
Upper tail coverts	chestnut; few black spots or bars	chestnut to buffy white	rufous or chestnut, marked with black	black
Outer rectrix pattern	rufous with black base and spots in some	mainly rufous, base black; or rufous with dark spots	rufous and black barred or like *elegans*	black; white tip and trace of white bars
Pattern and color of secondaries	chestnut; barred, spotted or unmarked	chestnut-rufous; bars on inner vanes	rufous fully barred with black or brown	black and white barred
Bill color	pale	pale	dusky, often pale tipped	blackish

[a] There is of course more variation than can be summarized here; see text.

shows great variation in dorsal barring, from unbarred (some *C. f. ochraceus*) to fully barred (*C. f. flavescens*). Indeed, the extent of dorsal barring varies in *C. castaneus*, some specimens being heavily barred, most showing moderate barring, and some (e.g., AMNH 326644) having narrow bars. The secondaries of *C. flavescens* and *C. lugubris* are barred, and those of *C. elegans* vary from moderately barred on the inner vanes

to unbarred (some *C. e. citreopygius*, e.g., AMNH 231571). *Celeus castaneus* is illustrated in figures 2 and 3.

The rectrices of *castaneus* are unusual in the *elegans* group in that the bases are rufous, as in *C. grammicus*. However, the outer (sixth) rectrices are black basally, and patterns of these feathers resemble some of the variant patterns found in outer rectrices of *C. elegans*. The unbarred yellowish area on the sides of *castaneus* resembles that of *elegans* (also *grammicus*). *Celeus castaneus* is moderately crested, resembling generally the *elegans* racial group of *C. elegans*. Furthermore, the individual variation within *C. elegans hellmayri* and geographical variation among races (*approximans*, *hellmayri*, *leotaudi*) of the *elegans* subspecies group of *C. elegans* are matched by the individual variation in color of crown and crest of *C. castaneus*. Some birds have a chestnut crown and crest nearly concolored with the back, others are mixed cinnamon and blonde, and some are pale cinnamon-buff. The pale, often black-based, bill of *castaneus* is similar structurally and in color to that of *C. elegans*; indeed smaller individuals of the latter exactly match some specimens of *castaneus* in bill color and structure.

Celeus castaneus, because of its small size, broad red facial markings of males, barred underparts and dorsum, and rufous base of the tail, might be considered more closely allied to *C. grammicus* and *C. undatus*, or to *C. loricatus* because of these features. *Celeus castaneus* differs from *loricatus*, with which it is sympatric, in having a curved culmen and less pronounced nasal ridges, unbarred yellowish flanks, long crest, and unbarred throat, crown, and rump. From *grammicus* and *undatus*, *castaneus* differs in having a longer crest, unmarked throat, relatively unbarred secondaries, and in a proportionally larger (longer, deeper) bill, resembling more closely that of other species of the *elegans* group. Similarities to *grammicus*, *undatus*, and *loricatus*, and to Asian *brachyurus* suggest that *castaneus* may resemble more nearly the ancestor of the superspecies *elegans* than do the other allospecies.

Celeus [*elegans*] *elegans* (P. S. L. Müller)

This species is comprised of a number of moderately distinct races, arranged in two groups, the long-crested *elegans* of northeastern South America, and the short-crested *jumana* from the Amazon-Orinoco region. The *elegans* racial group (subspecies *elegans*, *leotaudi*, *approximans*, *hellmayri*, *deltanus*) exhibits great variation in crown and crest color, as well as in body size. The *jumana* group consists of two distinct races, eastern *jumana* which is paler and shows much evidence of barring dorsally and in the wings, and western *citreopygius*, a slightly darker form with much reduced

barring. The *jumana* and *elegans* groups interbreed (specimens in the American Museum of Natural History collection) in eastern Venezuela and probably along much of the area of contact shown in figure 1; they do occur without signs of interbreeding on opposite sides of the broad lower Amazon River. Their hybridization is in need of further investigation.

Generally, *C. elegans* is the most rufous-chestnut of all species of *Celeus*, because the ventral coloration is fully as dark as the back, and because the dark markings are reduced in size and limited in extent (table 1). The bill is pale, like that of *castaneus*, but otherwise resembles the bill of *C. lugubris* and *C. flavescens*. The barring of the back found in many specimens of both groups is like the back barring of *C. lugubris*. The tail is black, like that of *flavescens* and *lugubris*, and patterns of the outer (sixth) rectrices of some of *lugubris* resemble the typical pattern of *C. elegans*. The paler crested individuals of the *elegans* racial group have a crest identical to that of *C. flavescens* and *C. lugubris*. Except for some resemblance to *C. flavus* (see above), *C. elegans* is not particularly like any species outside of its superspecies. *Celeus elegans jumana* is shown in figures 2 and 3.

Within the *C. elegans* superspecies, *elegans* probably is the largest species (wing length to 173 mm. or more). *Celeus elegans* and *C. flavescens* have slightly longer tails (tail/wing ratios average 0.60 to 0.61) than *C. lugubris* (0.58 to 0.60) or *C. castaneus* (0.57). In contrast to *C. lugubris* and *C. flavescens*, *elegans* shows sex reversal (Short, 1970b) in tail and wing length. That is, females of *elegans* have slightly shorter bills and legs than males, but their wings and tails average 1.55 mm. longer (wing length greater in four of four samples with mean differences from 1.03 to 2.17 mm., and tail length greater in four of four samples with mean differences from 0.40 to 2.80 mm.). Maximum wing lengths of females exceed those of males by 5 mm., and in tail length several females exceed males by up to 8 mm.

Implications of the back barring evident in so many eastern specimens of *C. elegans* are discussed below.

Celeus [*elegans*] *lugubris* (Malherbe)

This woodpecker, which essentially occurs in the chaco and its fringes, is comprised of two minor races: *kerri*, a slightly larger, blacker race to the south (reaching north to southern Mato Grosso, although northern Paraguayan and southern Mato Grosso birds tend toward *lugubris*), and *lugubris*, a smaller, more rufous race to the north (eastern Bolivia, west-central Mato Grosso). The species resembles *C. flavescens* rather closely (table 1), especially the blacker *C. l. kerri*. The differences between *lugubris* and *flavescens* are in the direction of *elegans*, thus rendering *lugubris* somewhat

intermediate between *flavescens* and *elegans*. *Celeus lugubris* is barred black and whitish above, the white bars being narrower than in *flavescens*. The dorsal and ventral blackish coloration is never fully so black as in *C. flavescens flavescens*, for there is a sooty or even rufous cast. The head is "blonde," like *flavescens*, but dark patches about the eyes, lores, and ear coverts are more prevalent in *lugubris*. *Celeus lugubris* differs from *C. flavescens* (table 1) in having rufous and black, rather than white and black barred secondaries, rufous rather than black upper tail coverts, and rufous and black rather than black or black and white outer (sixth) rectrices. As a species *lugubris* is the smallest of the South American allospecies of the *elegans* superspecies, although *C. flavescens ochraceus* and *C. elegans leotaudi* are as small or smaller. I have described elsewhere (Short, 1970a) some aspects of the biology of *Celeus lugubris kerri*, which is depicted in figures 2 and 3.

Resemblances between *lugubris* and *elegans* include the rufous-chestnut coloration evident in the tail coverts, outer rectrices, secondaries, and most body feathers of *lugubris*, especially northern *C. l. lugubris* which is in secondary contact with *elegans* (hybrids occur; see below). Some of the unbarred rufous and black outer rectrices of *lugubris* match patterns of *elegans* and *castaneus*. In relative length of bill and tarsi (table 2) *lugubris* resembles *flavescens* more than *elegans*. The bill and tarsi of *lugubris* are as long as those of *elegans* (i.e., *C. e. hellmayri*, *C. e. jumana*), although *lugubris* has considerably shorter wings and tail than in *elegans*. *Celeus flavescens ochraceus*, the smallest race of *flavescens*, is similar to *lugubris* in wing and tail length, and the bill and tarsi also match those of *lugubris*. As in *C. flavescens*, the males and females of *lugubris* are essentially alike in wing and tail length, but females have slightly shorter bills and tarsi than do males. The bill of *lugubris* is variable in color, but invariably shows some black basally; some birds have a fully black bill.

Celeus [*elegans*] *flavescens* (Gmelin)

In pattern the most distinct species of the *elegans* group is *C. flavescens* (table 1). Strongly divergent extreme races occur in northeastern Brazil, and from southeastern Brazil to eastern Paraguay, and a third, intermediate subspecies (*intercedens*) inhabits the intervening area. The southeastern form, *flavescens*, resembles *C. lugubris kerri* (see figs. 2, 3), but is black below without sooty or rufous tinges, and broadly barred with black and white above. Its head and long crest are almost immaculate creamy white. Large in size, *C. f. flavescens* nearly attains a wing length equal to that of *C. elegans*, and its bill and tarsi are longer than those of any other species of the superspecies *elegans*. The northeastern race,

TABLE 2

A Mensural Comparison of Males of Adjacent and Contacting Forms of *Celeus elegans*, *Celeus flavescens*, and *Celeus lugubris*[a]

Form	N	Mean	SD	SE	Range	CV
			Wing Length			
C. e. jumana	12	157.58	6.71	1.94	144–167	4.26
C. f. ochraceus	7	143.43	2.23	0.84	141–147	1.55
C. f. flavescens	7	155.86	3.89	1.47	152–162	2.50
C. l. kerri[b]	6	146.16	3.06	1.25	142–150	2.09
C. l. lugubris	7	142.86	3.13	1.18	138–146	2.19
			Tail Length			
C. e. jumana	12	96.08	3.58	1.03	89–100	3.72
C. f. ochraceus	5	84.80	3.03	1.36	80– 88	3.58
C. f. flavescens	7	91.14	3.39	1.28	88– 98	3.72
C. l. kerri[b]	6	84.50	1.64	0.67	82– 86	1.94
C. l. lugubris	6	85.83	2.79	1.14	83– 91	3.25
			Bill Length			
C. e. jumana	12	22.69	1.09	0.31	21.2–24.5	4.79
C. f. ochraceus	9	21.00	0.82	0.27	20.1–22.7	3.89
C. f. flavescens	9	25.57	1.53	0.51	23.4–27.9	5.99
C. l. kerri[b]	6	22.62	0.45	0.18	22.0–23.2	1.98
C. l. lugubris	7	22.21	0.62	0.23	21.2–23.0	2.78
			Tarsal Length			
C. e. jumana	12	24.56	1.33	0.38	22.9–26.7	5.41
C. f. ochraceus	9	24.32	1.33	0.44	22.7–25.9	5.45
C. f. flavescens	10	27.46	0.97	0.31	26.3–28.8	3.53
C. l. kerri[b]	6	25.80	0.54	0.22	25.3–26.7	2.08
C. l. lugubris	7	25.06	0.70	0.26	24.1–26.0	2.79

[a]Specimens taken April to August from regions adjacent to areas of contact between: *C. e. jumana* and *C. f. ochraceus; C. f. flavescens* and *C. l. kerri;* and *C. l. lugubris* and *C. e. jumana*. See text. Measurements are in millimeters. N, sample size; SD, standard deviation; SE, standard error of mean; CV, coefficient of variability.

[b]For *kerri* only eastern Paraguayan birds are included.

ochraceus, has reduced dorsal barring; the bars are chevron-shaped or occasionally birds are unmarked (see figs. 2, 3). Dorsal coloration is rusty cream with a rust-tinged or blonde head and crest. In ventral coloration *ochaceus* shows rufous or sooty mixed with black, approaching the condition found in *C. lugubris*. This form is smaller than *flavescens*, with

measurements matching those of *C. l. lugubris*. The intermediate race, *intercedens* is variable, but in general resembles *flavescens* below, has intermediate dorsal barring (white bars broader than *flavescens*, but fully barred), and has some of the dorsal rust tinge of *ochraceus;* it is intermediate in size.

All forms of *flavescens* have black upper tail coverts, and black and white outer rectrices. The lack of rufous in these areas distinguishes even *ochraceus* from *lugubris*. This species shows fewer blackish facial markings so prominent in *lugubris*. The black, when present on the head, is limited to the loral region in *flavescens*, but tends to occur more regularly in *ochraceus*, in which it often reaches the suborbital region (but not the ear coverts as in many *lugubris*). The bill of *flavescens* generally is entirely blackish, although it may show some paler (horn) color as is the case of *lugubris* (*castaneus* and *elegans* are fully pale-billed). Thus, *flavescens* shows the greatest resemblance to *C. lugubris*. However, *C. f. ochraceus* does tend somewhat toward *C. elegans*. If we consider *C. castaneus* to be the species of the *elegans* superspecies most resembling the ancestor of that group (*castaneus*, with its rufous color and barring, resembles other, related species of *Celeus* more than do other allospecies of the *elegans* group), then *flavescens* seems to be more divergent from that ancestor than *elegans* and *lugubris*, that is, *flavescens* shows more derived characters than do those other species.

INTERACTIONS BETWEEN *CELEUS ELEGANS* AND *CELEUS LUGUBRIS*

The evidence for interbreeding between *Celeus elegans* and *C. lugubris* is of two sorts. The first is the general convergence of *lugubris* toward *elegans* at the northern end of its range, that is, where it approaches *elegans*. The second is the existence of two or three putative hybrids of *lugubris* x *elegans*.

The more rufous coloration of *Celeus lugubris lugubris*, compared with the blacker *C. l. kerri* from farther south, and the reduced barring (and hence more rufous color) in the secondaries of *C. l. lugubris* represent distinct tendencies toward *C. elegans*. Although the traces of barring (occasionally weak but extensive barring) occurring frequently in *C. e. jumana* and in the *elegans* group of *C. elegans* would appear at first glance to be unrelated to the distribution of *lugubris*, evidence presented by Haffer (1969) suggested the possibility of past extensive contact and hybridization of *lugubris* with both the *jumana* and *elegans* groups. Briefly, Haffer has indicated that, in the late Pleistocene, savanna, and bordering "edge" woodland, extended from the campos of central Brazil (the range of *lugubris*) across the lower Amazon and northward to Venezuela. The

TABLE 3

A COMPARISON OF *Celeus elegans*, *Celeus lugubris*, AND HYBRID

(Measurements in Millimeters [a])

Form	N	Wing Length Mean (range)	Tail Length Mean (range)	Bill Length Mean	Tarsal Length Mean	Pale Back Bar Depth	Secondary Bar Depth
C. e. hellmayri	5	161 (156–164)	98 (96–100)	23.18	25.20	0–traces	No bars
C. e. jumana	12	155 (149–160)	92 (87– 98)	22.80	24.55	0–traces	No bars
Hybrid[b]	1	148	92	23.6	25.0	2.0	6.1
C. l. lugubris	5	143 (139–148)	86 (81– 92)	21.90	25.00	2.64	2.81

		CONDITION OF OUTER RECTRICES				
		Fully Barred	Partly Barred	Rufous, Black Base	Black, Rufous Tip	Rufous, 1–4 spots
C. e. hellmayri	30	0	0	24	0	6
C. e. jumana	182	0	0	156	16	10
Hybrid	1	—	1	—	—	—
C. l. lugubris	16	11	1	4	0	0

[a]For mensural comparison only seasonally comparable adult males were used. N, sample size.

[b]The hybrid is NHMW 57531; see text.

elegans and *jumana* racial groups of ancestral *C. elegans* presumably were separated by this savanna intrusion, and came to occupy wet forest refugia respectively northeast (Guianas) and west (upper Amazon) of the extended savanna. *Celeus lugubris* may have spread northward through the more wooded portions of the savanna and along its fringes. Extensive hybridization and introgression could have occurred between *lugubris* and *jumana* to the west, and *lugubris* and *elegans* to the east. The rufous prevalent in *Celeus lugubris lugubris*, the dark dorsal barring so frequent in both the eastern populations of the *jumana* group and in the *elegans* group, and the long, pale crest of some populations of the *elegans* group could be aftereffects of introgressive hybridization. It is noteworthy that *C. elegans citreopygius* of western Amazonia, found so far west of any ancient contact with *lugubris*, shows little or no trace of barring dorsally and less blackish on its outer (sixth) rectrices than do the eastern races of *C. elegans*. Another possibility is that *C. lugubris* occupied the western fringe of the savanna area and hybridized with the *jumana* group of *C. elegans*, whereas *C. flavescens* (ancestral *C. f. ochraceus*) occupied the eastern savanna fringe and hybridized there with the *elegans* group of *C. elegans*. The latter possibility would account for the features of *lugubris*, and of the *elegans* and *jumana* racial groups noted above, and it would also explain the rufous tendency of *ochraceus* as a parallel to that of *lugubris*.

The above suggestions correlate well with the narrow sympatry and likely interactions between *Celeus elegans jumana* and *C. flavescens ochraceus* in Pará and probably Maranhão, and with the occurrence of two or three possible hybrids of *Celeus e. jumana* and *C. l. lugubris* in Mato Grosso. One of these likely hybrids is male NHMW 57531. This specimen was obtained by Natterer on September 23, 1828, in the vicinity of Mato Grosso, on the upper Guapore River in west central Mato Grosso (near Chapada). Its label bears an unsigned comment "zwischen *elegans* und *jumana*," a most unlikely cross because populations of the *elegans* racial group do not occur within 1500 km. of the town of Mato Grosso. This male is the type of *Celeus reichenbachii* described by von Pelzeln (1870), who suspected it was a young bird, partly because of its short wings. Naumburg (1930, p. 183) referred to this specimen in a footnote in which she mentioned Hellmayr stating (*in litt.*) that it differs from *C. e. jumana* "in having the forehead and crown buffy yellow, mesially streaked with rufous brown." Examination of the specimen indicates that it is not an immature bird, but an adult.

Measurements of this specimen are given in table 3, in which it is compared with 12 seasonally comparable males of *Celeus elegans jumana* taken south of the Amazon (chiefly along the Rio Tocantins), and five comparable Mato Grosso specimens of *C. l. lugubris*. In wing length the

putative hybrid falls within the range of *lugubris*, but at its upper extreme, and just below the range of *jumana*. The presumptive hybrid falls within the *lugubris-jumana* overlap area in tail length, bill length, and tarsal length (table 3). Generally it tends slightly toward *jumana* in tail length and bill length, and perhaps toward *lugubris* in tarsal length. There is no evidence from the mensural data (see also table 2) that precludes the specimen representing a hybrid, and, indeed it tends to be intermediate in tail length and especially in wing length.

The specimen looks more like *jumana* than like *lugubris*. However, it tends toward *lugubris* in a number of features, and in some of these it exceeds the variation found in *jumana*. As noted above, many specimens of *Celeus elegans jumana* show signs of dorsal barring. The specimen in question resembles the more strongly barred variants of *jumana*. Although the pale bars are partly obscured by rufous coloring, they are visible, and measure about 2 mm. in depth. The back bars of *lugubris* (table 3) average 2.64 mm. in depth. Thus, the barring of the putative hybrid may or may not represent a tendency toward *lugubris*.

The secondary feathers of *jumana* typically are rufous-chestnut with black barring restricted to the inner vanes, and which tends to be reduced distally and on the inner secondaries and tertials. *Celeus lugubris lugubris* has fully barred rufous and black secondaries. Both forms tend to have replacement of the rufous-chestnut by yellow-white toward the bases of the inner vanes. The putative hybrid is more strongly barred on the secondaries than any of the 212 specimens of *C. elegans* in the American Museum of Natural History collection. The dark barring is virtually complete on the inner vanes, and the outer vanes are from one-half barred (inner secondaries) to fully barred (outer secondaries). This barring represents a definite tendency toward the barred condition of *lugubris*.

The outer (sixth) rectrices of *C. elegans* are usually rufous with a black base, which varies in extent from small (180 of 212 specimens) to extensive (more than one-half the feather length in 16 specimens of the *jumana* group and none of the *elegans* group). Six specimens of the *elegans* group and 10 of the *jumana* group have these feathers rufous in color with one to four black spots. I have found no specimen of *C. elegans* that exhibits barring on the outer rectrices. *Celeus lugubris lugubris* is variable in color of the outer rectrices (table 3). Four specimens resemble *C. elegans* in the pattern of these feathers, but 12 are partly or fully (11 of 12) barred rufous and black. The questionable specimen has rufous outer rectrices which are asymmetrical in their patterns, but the left and right feathers show partial bars. The bars are very broad and extend toward the rachis from the feather edges, but only the basal bar of the four bars is complete across the rachis.

Near the tip of each feather, above the last partial bar are two small spots of black, recalling the variant condition of some specimens of *C. elegans*. This pattern is within the range of variation of *C. l. lugubris*, although not matching precisely that of any specimen of that form. The definite barring is unknown in *C. elegans*, thus arguing for the hybridity of the specimen.

The *elegans* group of *C. elegans* is long-crested, closely approaching and even equaling the crest length of *C. lugubris*. The *jumana* group is short-crested, however. On measuring the longest crest feathers (a measurement difficult to obtain, and not very exact), I found that unworn specimens of *Celeus lugubris* and of the *elegans* group of *C. elegans* had feathers exceeding 35 mm., whereas specimens of the *jumana* group of *C. elegans* had feathers usually 25 mm. or less. The maximum feather length I could obtain for *C. e. jumana* was 27 mm. The putative hybrid has a crest the feathers of which attain a length of 30 mm. Furthermore, the anterior crown feathers of this specimen are longer and tend to be pointed, thus adding to the crest, whereas *C. e. jumana* has shorter, less pointed crown feathers. Specimen NHMW 57531 thus is intermediate in the length of its crest. As noted above, the crown of this bird is peculiar in color. Feathers of the forehead and anterior crown are rufous-centered with broad "blonde" edges and tips. About half of the hind-crown feathers, that is, those comprising the crest itself, have blonde edges and tips. Several of these crest feathers are fully barred black and buffy on one vane. This latter condition and, indeed, blonde or buff-coloring and barring are unknown in *C. e. jumana* (the comparison includes juvenile birds, and adults, so there is no indication of age variation). Specimens of *C. lugubris* typically have white, buff or blonde crests, and the feathers are black at the base; occasionally there is a dark bar above the black base. Generally, the color as well as the shape of the crest (and crown) feathers of the specimen in question is intermediate between *lugubris* and *jumana*.

The specimen exhibits more ventral barring, particularly on its sides and abdomen, than do specimens of *C. elegans*. The extent and blackness of the barring closely approaches *C. lugubris*, and exceeds variation in *elegans*.

The village of Mato Grosso near where the putative hybrid was taken, is close to Chapada, from which I have seen three specimens (see below) of "*lugubris*." I believe that the Mato Grosso specimen represents a hybrid of *C. e. jumana* x *C. l. lugubris*. If it is not a hybrid, it must stand as a most aberrant specimen of *jumana*, tending in several ways toward *lugubris*, and representing a locality within the known range of *lugubris*. The nearest locality for *C. e. jumana*, other than that represented by the putative hybrid, is Monte Cristo, somewhat to the northwest (AMNH 127512).

There are two other possible hybrids of *jumana* and *lugubris*. Both are females from localities at the northern extreme of the range of *lugubris*, where contact with *jumana* might be expected. Indeed one of these, AMNH 34294, comes from Chapada, just northeast of the town of Mato Grosso, where it was collected in March, 1885. The other, AMNH 127134, comes from Tapirapoan in north-central Mato Grosso, where it was taken on January 17, 1914; it is the type of *Celeus roosevelti* Cherrie (1916). Both specimens were noted as possibly immature by Naumburg (1930); I doubt that AMNH 127134 is an immature specimen although the other might be. Molting birds can be aged by the molting of secondaries, which occurs only in adults. However, the molt must have progressed far enough to have resulted in molt of some secondaries in adult birds. Unfortunately, both questionable specimens are at too early a stage of molt (innermost primaries beginning to molt) for the secondaries to be molting. However, compared with undoubted juveniles of *C. flavescens ochraceus*, *C. elegans jumana*, *C. lugubris kerri*, and *C. l. lugubris* (AMNH 149470), neither of the problem birds appears clearly to be in juvenal plumage. Juveniles of the pale-crested forms usually show some black or brown in the crest, and the barred forms have narrow pale dorsal bars. Neither of the problem specimens is so marked. However, the age of these specimens is not important, as noted below, because their hybrid features involve characters seemingly not affected by age.

The two females in question differ from *lugubris* in their very cinnamon-rufous overall color, most prominently shown in the superficially unbarred, rufous secondaries. Actually, these feathers are barred on the inner vanes, but the barring is absent toward the feather tips and on the outer vanes; in other words, the secondaries are colored as in *C. elegans jumana*. AMNH 127134 far exceeds the other specimen in the extent of its rufous coloration. Its dorsal dark barring, ventral and lower throat color are predominantly rufous. Black can be seen only in some of the wing covert barring, and in the barring on the sides. Both specimens have very buffy, rather than cream-colored heads, especially on the sides of the neck. AMNH 34294 shows rufous centers in some crown feathers. As to their possible immaturity, there is no evidence that immature individuals of *lugubris* are more rufous and less barred on the secondaries than are adults. Immature specimens of the rufous *C. elegans jumana* if anything tend to be more barred on their secondaries than are adults. Immatures of *Celeus flavescens ochraceus*, which tend to be somewhat cinnamon or even rufous, are no more rufous, and certainly no less barred than are adults. AMNH 149470, which by plumage texture and narrowed white barring above appears to be a juvenile of *C. l. lugubris* has fully barred rufous and brown secondaries.

Thus, whether the two questionable birds are immatures (AMNH 34294 is more likely to be such), there is no reason for their very rufous coloration to be ascribed to immaturity. I should note that females of *C. l. lugubris* tend to be more variable than males, and they generally show more rufous overall than do males.

The outermost rectrices of both specimens are in the intermediate range between *C. elegans jumana* and *C. l. lugubris*. AMNH 34294 has black-based outer rectrices, with a single pale half-bar, and five variably sized black spots toward the tips of the asymmetrically marked feathers. Only a single outer rectrix is present in AMNH 127134, and it is about one-half grown; the feather is totally rufous for the visible half of its length, thus resembling most *jumana* and one-quarter of *lugubris* specimens.

Mensurally AMNH 34294 is about average in wing length and tail length for *C. l. lugubris*, and shows no tendency toward *C. e. jumana*. However, AMNH 127134 is extreme among specimens of *lugubris*, and hence tends toward *jumana*, as shown by these data (seasonally comparable females, measurements in mm.):

Form	N	Wing Length		Tail Length		Bill Length
		Range	Mean	Range	Mean	Mean
C. e. jumana	6	153–161	156.33	91–95	92.40	22.53
AMNH 127134	—	146	—	94	—	21.7
C. l. lugubris	6	138–146	141.00	80–88	84.20	21.24

This specimen is at the upper extreme for *lugubris* in wing length. In tail length it falls well above the range of any specimen of *lugubris* (both sexes), even those in fresh plumage; indeed it is above the average for *jumana*. Because of the great overlap in bill length between the slightly longer billed *jumana*, and *lugubris* (see table 2), no significance is placed on the fact that the bill length of the specimen in question falls between the means of the two forms. On the basis of analysis of mensural and color features AMNH 127134 seems to be a hybrid; the other questionable female could represent a hybrid, an introgressant *lugubris* (or a backcross product of a hybrid x *lugubris*), or an extreme variant *lugubris*.

The fact that these two females, as well as the hybrid male discussed above come from the northern extreme of the range of *C. l. lugubris*, where that form is likely to meet *C. elegans jumana*, makes hybridity and introgression rather than extreme individual variation more likely for their tendencies toward *jumana*.

The sample of three specimens from Chapada, very close to the town of Mato Grosso, is interesting in view of the occurrence of two of the four putative hybrids among the four birds known from these two localities.

The hybrid male from Mato Grosso, which resembles *jumana* more than *lugubris*, was discussed above, as was female AMNH 34294, which is very rufous, but otherwise approaches *lugubris*. Female AMNH 34295 is a moderately rufous bird, about average for *lugubris* females and fully barred on its secondaries. Its outer rectrices are somewhat more barred than are those of 34294, but the pattern is strongly reminiscent of the pattern of the latter bird. Ventrally it is somewhat less rufous than is 34294. Male AMNH 34298 contrasts strongly with the other three specimens; indeed, it is so black that it essentially matches *C. l. kerri* (its measurements are within the range of overlap of *lugubris* and *kerri*). These specimens stress the slight differences between *kerri* and *lugubris*, which may be characterized as more variable, more rufous and slightly smaller than *kerri*. They also suggest three points concerning *lugubris* and *jumana*, namely, that interbreeding does occur between these forms, that the interbreeding is not complete (random), and that present or past interbreeding of these forms may be responsible for the rufous coloration of *lugubris*, as opposed to the more southern *kerri*.

In summary, *Celeus lugubris lugubris* sporadically meets and occasionally hybridizes with *C. elegans jumana*. Two, and possibly three hybrids are known. Interbreeding appears not to be "free," although more specimens are needed to determine its extent. Introgression as a result of present or past interbreeding of *lugubris* with *jumana* may be responsible for the tendency of *C. l. lugubris* toward *jumana* and away from *C. l. kerri* in coloration.

INTERACTIONS AMONG *CELEUS LUGUBRIS* AND *CELEUS FLAVESCENS*

The range of *Celeus lugubris* approaches that of *C. flavescens* in eastern Paraguay and northeastern Argentina. Within Argentina *flavescens* seems restricted to the diminishing forests of Misiones; it does not appear to occur in the restricted riparian forests along the Uruguay and Upper Parana rivers in Corrientes. *Celeus lugubris* enters Corrientes from the chaco, occurring in the woodlands of western Corrientes and eastward at least halfway across Corrientes along the Upper Parana River (see Short, In press a). Misiones specimens of *flavescens* and the few Corrientes specimens of *lugubris* show no indications of the effects of hybridization or introgression. The Corrientes specimens of *lugubris* include two birds from the vicinity of Itá-Ibaté (in the American Museum of Natural History), a male from the "Parana River" (USNM 16399, July, 1859, Capt. T. J. Page Expedition, locality uncertain), and two females from Itatí (in Museo de Ciencias Naturales, Buenos Aires). Another Page specimen (ANSP 19560) dated January 8, 1955, and labeled "Corrientes," is a

juvenal bird; it is discussed below. Noteworthy too are two females of *kerri* (SM 31896, 31897), which with two females of *flavescens* (SM 31911, 31912) in the Fritche collection of the Senckenberg Museum are labeled "Pto. Bermejo." This locality, at the mouth of the Bermejo River, northeastern Chaco, is situated not far north of the junction of the Upper Parana and Paraguay rivers. There are no dates on the labels of the four specimens, but it is likely that at least the *flavescens* specimens were taken other than at Puerto Bermejo, that is, across the Paraguay River some distance into eastern Paraguay, or at some point in extreme eastern Corrientes (?) or in Misiones, along the Upper Parana River. In view of the lack of sympatry of *flavescens* and *kerri* elsewhere (see below), it is not appropriate to infer their sympatry from the four "Pto. Bermejo" specimens. No indications of hybridization are evident in the four specimens.

Available from eastern Paraguay were specimens of *kerri* from these localities: Aregua, Rosario, Horqueta, Concepción, Villa Elisa (20 km. S Asunción), Bernalcué (near Asunción), Colonia Nueva Italia, 40 km. WSW Capitán Bado, Zanja Morotí, Belén, and San Luis de la Sierra. Specimens from "Riacho Negro" and "Puerto Gibaja" are probably from somewhere in eastern Paraguay, but their exact location is uncertain (see Short, In press b). Specimens of *C. flavescens flavescens* from eastern Paraguay are few in number, and come from: east of Caaguazú, and Colonia Independencia (near Villa Rica). These localities for *flavescens* are the farthest western records of this form, otherwise known in Paraguay only along the Upper Parana River opposite Misiones. Both localities are at the edge of the Paraguayan highlands. *Celeus lugubris kerri* is known from these highlands in northern Paraguay (Capitán Bado area), but in southern Paraguay it is known only from the vicinity of the Paraguay River (presumably also along the Upper Parana River east as far as Itá-Ibaté, Corrientes, whence come specimens south of that river). The farthest inland records are those from Sapucay and Ibitimi (Chubb, 1910). The last locality is 50 km. west of Colonia Independencia, the westernmost locality for *flavescens*. Not one specimen of either form from eastern Paraguay is a possible hybrid; all fall within the range of variation of one or the other form. As I have noted elsewhere (Short, In press a), the supposed occurrence of *flavescens* and *kerri* together at Villa Elisa (Olrog, 1963) is erroneous; the two specimens referred to by Olrog both represent *kerri*. Hence, existing data provide no indication that the two forms are in contact, although this is likely. The lack of indications of hybridization in the specimens examined suggests that hybridization is infrequent and local in occurrence, if indeed it does occur.

A comparison of 36 eastern Paraguayan and northern Corrientes speci-

mens of *kerri* with 13 western Paraguayan and eastern Chaco, Argentina, specimens of this subspecies was undertaken to determine whether eastern birds varied toward *flavescens*. I found that the two samples were not significantly different in measurements or in color characteristics. The only tendency observed that could be construed as an indication of gene flow between *kerri* and *flavescens* is the more white, less dark-marked head of eastern birds. Twelve of 13 chaco specimens showed brown color extending from the lores suborbitally into the ear coverts. In contrast, only 15 of 35 eastern birds showed dark coloration as far posteriorly as the ear coverts. Likewise, more chaco birds showed black gular color (four of 12) and connection of the dark malar color with the throat (10 of 12), than was true of eastern birds (three of 34 with black in gular, 10 of 34 with throat-malar connection). Eastern specimens also exhibited more barring on the upper tail coverts than western birds, but this cannot be a tendency toward *flavescens*, which uncommonly has barred upper tail coverts. In the absence of other evidence for introgression, and considering the small size of the chaco sample, the variation in color of the head of birds in the two samples cannot constitute an indication of introgression.

It might be noted that all Paraguayan specimens of *C. lugubris* examined are referable to *kerri*. Influence of *lugubris* is evident in northeastern Paraguayan birds (from Horqueta north, including Zanja Morotí and San Luis de la Sierra; also Puerto Casado specimens), especially in their rufous tendency ventrally, but in size and most color features these birds are nearer *kerri*. A specimen from General Diaz, far north in western Paraguay, is typical of *kerri*.

Only two specimens have been seen which conceivably could represent hybrids of *flavescens* and *lugubris* (*kerri*). One of these is a juvenal male (ANSP 19560) mentioned above from "Corrientes." This specimen is peculiar for *kerri* in two respects, namely tail length (91 mm.) and pattern of the sixth rectrices (see tables 2, 3). It has a longer tail than all adult specimens of *kerri* examined. Its outer rectrices have a mainly black pattern with a rufous tip and small indentation into the subterminal black area; this pattern resembles the common pattern of *flavescens*, except that in *flavescens* the pale area is white, not rufous. In view of the fact that the upper tail coverts, color of secondaries, ventral coloration and back-barring are typical of *kerri*, I prefer to regard the long tail of this aberrant specimen as a result of extreme variation in *kerri* (specimens of *C. l. lugubris* sometimes do attain a tail length of 91 mm.), and the outer rectrix pattern as an extreme variant pattern perhaps resembling that of some ancestral species.

The other possible hybrid is an adult male (MCZ 154591) from

Miranda, southern Mato Grosso. This specimen generally resembles northern Paraguayan specimens of *kerri* > *lugubris*. Mensurally the questionable bird does not exceed *kerri*; its bill at 23.1 mm. is longer than that of most specimens of *C. lugubris* (table 2), but it is not within the range of variation of *C. flavescens*. In coloration, however, it exceeds variation of *C. lugubris* in back barring and in the upper tail coverts. It also is extreme for *lugubris* in the color of its secondaries. The back of the Miranda specimen is rather broadly barred with white and gray-black. The white bars are exceptionally broad throughout, rather than being broad at the rachis and tapering to very narrow at the feather edges as in most specimens of *lugubris*. The white bars are 3.7 to 3.8 mm. in depth, exceeding *lugubris* as well as *kerri*, and falling within the range of *flavescens*. The upper tail coverts are barred black and mixed white and rusty, with more white evident than in any other specimen of *lugubris* and *kerri* (one bird, AMNH 319717 from Zanja Morotí, Paraguay, is considerably white, especially in the outer coverts, but it is not nearly so white as is the Miranda bird). Other noteworthy features of this specimen are its secondaries, which show much white (although they are more rufous than white), and white dorsally, which has a somewhat yellowish cast. Ventrally its coloration is like northern specimens of *kerri*, that is, sooty black with a rusty cast. Its outer rectrices bear a pattern typical (barred rusty and black, although showing some white mixed with the rust color) of *Celeus lugubris*. Overall, this bird resembles *C. lugubris kerri* > *lugubris* more than it resembles *C. flavescens*, but its tendencies toward the latter species in several characters suggest that it could represent a backcross product of an F_1 hybrid with *C. lugubris*. However, its measurements are not indicative of hybridity. Furthermore, although Miranda is in south-central Mato Grosso, it is far from a possible contact with *C. flavescens*. The latter is known to occur along the Upper Parana River in southeasternmost Mato Grosso. Localities listed by Pinto (1938) under *C. f. flavescens* are Jupia (actually in São Paulo on the east bank of the Parana River), Rio Paraná, and Sant' Anna do Paranaiba (the latter is very near Goiás and could represent *C. f. intercedens*, but I have not seen specimens). No woodpeckers of these species are known from Mato Grosso east of a line from Cuiabá south to Miranda, and west of about 25 km. west of the Parana-Paranaiba rivers (much farther north in northeastern Mato Grosso, *C. f. intercedens* is known to occur along the Rio dos Mortes). There appears to be no opportunity for contact between western Mato Grosso *C. l. lugubris* and Goiás *C. f. intercedens*, and the possibility of a contact between *C. flavescens* and *C. lugubris* in southeastern Mato Grosso is not great, although this may only reflect a lack of collecting in these regions.

Pending investigation of possible areas of contact, I prefer to treat the two problem specimens as aberrant individuals of the variable *Celeus lugubris kerri*. The general convergence of northern *C. l. lugubris* toward *C. elegans*, and of southern *C. l. kerri* toward *C. flavescens* is interesting. The relation of these convergences to past hybridization is of course a matter of speculation. We do know that *lugubris* hybridizes with *elegans* at least sporadically, possibly with some introgression occurring today; undoubtedly there was more interbreeding in the past. *Celeus lugubris kerri* may approximate in appearance the ancestor of *C. lugubris*, and indeed of *C. flavescens* as well; hence hybridization need not be invoked to explain the resemblance of *kerri* to *flavescens*.

INTERACTIONS BETWEEN *CELEUS ELEGANS* AND *CELEUS FLAVESCENS*

The larger *Celeus elegans jumana* extends eastward in Amazonia through Pará to the mouth of the Amazon, and beyond into Maranhão. It overlaps with the smaller *C. flavescens ochraceus* in Pará and Maranhão. Actual points of sympatry are: Baião on the lower Rio Tocantins; in the Serra de Parintins near Villa Bella Imperatriz on the south bank of the Amazon; and, Jeha Itauna (see Naumburg, 1935) on the Ilha de São Luiz, Maranhão. Baião is represented by two specimens of *ochraceus* (AMNH 430656, 430657) taken on Dec. 5, 1931, and one specimen of *jumana* (AMNH 430646) collected on Dec. 15, 1931. From the Serra de Parintins come one *ochraceus* (AMNH 278666) bearing the date Nov. 10, 1930, and two individuals of *jumana* (AMNH 278662, 278664) obtained Nov. 12 and Nov. 17, 1930. Seven other specimens of *jumana*, but none of *ochraceus*, bear "Villa Bella Imperatriz" on labels, but with localities other than the Serra de Parintins. The seven specimens of *jumana* were taken from August to November, 1930. Finally, Jeha Itauna is represented by one *ochraceus* (AMNH 242706) dated Feb. 10, 1926, and one *jumana* (AMNH 242686) taken on Feb. 12, 1926.

None of these or any other specimen of *jumana* and *ochraceus*, shows evidence of hybridity. Nor are there any indications of introgression in samples from the area of overlap. Rather it seems that limited sympatry occurs between these woodpeckers at least along certain rivers and in coastal Maranhão. Actual interactions between individuals of the two species have not been studied. It is worth noting those features of *ochraceus* in which it is more divergent from *C. elegans jumana* than is *C. lugubris lugubris*, as *ochraceus* fails to interbreed with *jumana*, whereas *lugubris* does so to a slight extent. Compared with *C. l. lugubris*, *C. flavescens ochraceus*, tends away from *lugubris* (and *C. e. jumana*) in having: blacker, less rufous

underparts; more nearly black rather than horn-colored or grayish bill; less rufous, more contrasting white and black upper parts; black and white, not rufous upper tail coverts, secondaries and outer rectrices; fuller buffy cream-colored head (less dark markings about the face); and, less barred primaries (see also table 1). Thus, in all of these features *ochraceus* is less like *jumana* than is *lugubris*. These differences between *ochraceus* and *lugubris* are such that *ochraceus* probably would be much more readily distinguishable from *jumana* than would *lugubris* under conditions of low light intensity, e.g., in the shade of a tree trunk. *Celeus flavescens ochraceus* nevertheless shows more buff and even rufous traces in its dorsal coloration and in its secondaries than does the more contrastingly colored *C. f. flavescens*. *Celeus flavescens ochraceus* hence is slightly convergent toward *C. elegans* and away from *C. f. flavescens*, but it does not resemble *elegans* nearly so much as does *C. l. lugubris*.

I do not believe that the size differences between northern *C. flavescens ochraceus* and *C. lugubris lugubris*, and, respectively, southern *C. f. flavescens* and *C. l. kerri* (table 2) represent character displacement of the northern forms as a result of their interactions with *C. elegans jumana*. Southern forms within a species generally tend to be larger in South America (personal observ.), presumably in accordance with Bergmann's Ecogeographic Rule, and so it is not unexpected that the southern races would show greater measurements. *Celeus lugubris* and *C. flavescens* have proportionally longer bills and tarsi than does *C. elegans*. The races of the former two species that come in contact with *C. e. jumana* retain these differences in proportions. Thus, although *lugubris* and *ochraceus* are smaller (judging from appearance of specimens and from wing length data) than *jumana*, they have a bill and tarsi equal in length to those of *jumana*. I conclude that *C. lugubris* potentially is capable of coexisting with *jumana*, just as is *C. flavescens ochraceus*. It is possible that the incomplete reproductive isolation of *lugubris* is the main factor preventing its sympatry with *jumana*.

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